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Invasive alien plants at Capraia Island (Italy): distribution and threats to Natura 2000 habitats

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Abstract

Island ecosystems face significant threats from biological invasions due to their unique biomes. In over a quarter of these ecosystems, the number of alien plants surpasses the total count of native ones, leading to notable impacts. This concern is particularly pronounced in the Mediterranean Basin, a globally important hotspot for plant diversity. In line with this, our study aimed to investigate the current distribution of six main alien plant species (*Chasmanthe floribunda*, *Nicotiana glauca*, *Opuntia ficus-indica*, *Opuntia stricta*, *Senecio angulatus*, and *Zantedeschia aethiopica*) on Capraia Island in the Tuscan Archipelago, Italy. We identified invaded vegetation types and N2000 habitats (*sensu* 92/43/EEC "Habitats" Directive), created a detailed map of the current distribution of these six target species, and analyzed the relationship between their distribution and environmental factors. The six target species were found to be more widespread in areas of the island with higher levels of anthropogenic disturbance, with only *O. stricta* also spreading into natural habitats. Overall, the invasion covers an area of 71 hectares (3.6% of the island's surface), of which over 70 hectares are invaded by *O. stricta*. The habitats most impacted by alien plant invasion include 5330 "Thermo-Mediterranean and pre-desert scrub", 5320 "Low formations of *Euphorbia* close to cliffs", 1240 "Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp.", and 6220* "Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*", all primarily invaded by *O. stricta*. Environmental factors most correlated with alien plant distribution include the distance from infrastructure, altitude, and slope aspect.

Keywords

Biological invasions, distribution map, management, Mediterranean ecosystems, Mediterranean island, *Opuntia stricta*

Introduction

Biological invasions represent one of the main causes of biodiversity loss at the global level, following habitat fragmentation and degradation (Seebens et al. 2017; IPBES 2023). There are more than 3,500 invasive alien species (IAS) with evidence of negative impacts and 20% of all impacts are reported from islands (IPBES 2023). Additionally, it is estimated that in more than a quarter of the islands, the number of alien plants exceeds the total number of native ones (IPBES 2023). Island ecosystems are, in fact, more vulnerable to alien plant invasion due to their peculiar ecological and biological traits, such as smaller populations, narrower ranges and lower genetic variability (Lonsdale 1999; Vila et al. 2006; Kueffer et al. 2010; Celesti-Grapow et al. 2016; Russell et al. 2017).

About 6% of all alien plants are considered to be invasive (IAPs), as they do represent a real threat to biodiversity, human health and economy, exerting numerous deleterious impacts at different levels (Kumar Rai and Singh 2020; Pyšek et al. 2020). In fact, IAPs can alter community composition and biotic interactions, inducing further cascade effects also on regulating services (Vilà and Hulme 2017), and leading to the biotic homogenization of ecosystems (Olden and Rooney 2006). In addition, from an economic perspective, the impacts can be very high. For instance, in Mediterranean Basin one third of the total costs ($17.76 billion) financed for the damage repair,

medical care and management of the IAS, is ascribed to alien plants (Kourantidou et al. 2021).

For this reason, the Convention on Biological Diversity CBD (http://www.biodiv.org) has repeatedly emphasized the primary importance of protecting higher-risk areas, placing special emphasis on biodiversity conservation and sustainable development on islands (Reaser et al. 2007). As one of the most important centers of civilization and trade activities in history, the Mediterranean Basin is exposed to a high invasion rate, and even more they are its numerous islands and islets (Gritti et al. 2006). Among its largest islands, Sardinia and Corsica have the highest percentage of alien plants, just over 17%, but with a great difference in the percentage of invasive plants, almost double in Corsica (21.2%) compared to Sardinia (12.6%). The other major islands, Sicily, Cyprus, Crete, and the Balearic Islands have lower numbers of alien taxa, ranging from 6.7 to 13.5% (Médail 2022). An increase in invasive alien species has also been reported for small Mediterranean islands, especially since the second half of the 20th century when tourism and anthropogenic pressures became more intense (Delanoë et al. 1996; Celesti-Grapow et al. 2016; Chiarucci et al. 2017; Carta et al. 2018). The most representative invasive plant families identified across 37 small Mediterranean islands are *Poaceae*, *Solanaceae*, *Amaranthaceae*, *Aizoaceae*, *Fabaceae*, *Cactaceae* and *Asteraceae*. Notably, the latter three families exhibit the highest number of invasive species, with the genus *Opuntia* being particularly noteworthy (Celesti-Grapow et al. 2016). Moreover, the species *Nicotiana glauca*, *Opuntia ficus-indica* and *Senecio angulatus* are the most widespread in the islands so much so that the last two mentioned and *Zantedeschia aethiopica* show a change in their invasion status (Celesti-Grapow et al. 2016). However, the distribution knowledge of the alien plants varies depending on the level of research efforts, and this variability may influence the assignment of invasion status. For example, the *Opuntia* genus (especially *O. ficus-indica*), *Senecio angulatus* and *Nicotiana glauca* species are the most mentioned and investigated in scientific articles and research, while, for example, *Chasmanthe floribunda* had been previously incorrectly reported as *Chasmanthe aethiopica* (L.) N.E.Br. concerning the Tuscan Archipelago (Galasso et al. 2021).

Focusing on the Tuscan Archipelago, Capraia is the third largest island, but the second as far as invasion rate is considered, after Elba, the largest one (Lazzaro et al. 2014; Carta et al. 2018). The main IAPs on this island are *Chasmanthe floribunda* (Salisb.) N.E.Br (*Iridaceae*), *Nicotiana glauca* Graham (*Solanaceae*), *Opuntia ficus-indica* (L.) Mill. (*Cactaceae*), *Opuntia stricta* (Haw.) Haw. (*Cactaceae*), *Senecio angulatus* L. f. (*Asteraceae*) and *Zantedeschia aethiopica* (L.) Spreng. (*Araceae*). *Chasmanthe floribunda*, *Senecio angulatus* and *Zantedeschia aethiopica* are native to South Africa, while *Nicotiana glauca* is native to South America and the two species of *Opuntia* come from Central America. All these IAPs show ecological traits linked to high invasiveness, such as high seed production, high vegetative reproductive capacity, and remarkable ecological amplitude and performance under constraining conditions (i.e. ability to conserve water, resist drought and salinity, and grow in disturbed areas) (Podda et al. 2017; Weber 2017). Moreover, *Senecio angulatus*, *Zantedeschia aethiopica* and *Nicotiana glauca* are toxic and potentially harmful to the health of animals and humans (Porter and Geissman 1962; Furer et al. 2011; Weber 2017). Furthermore, they all are able to form dense monospecific populations that prevent the establishment of native species (Weber 2017). Although all of them have ecological characteristics that favor their spread at the expense of native species, they show different degrees of invasiveness. In fact, all are locally considered as invasive except for *Chasmanthe floribunda*, which is considered as naturalized (Lazzaro et al. 2014).

Capraia, like the other islands of the Tuscan Archipelago, is included in the N2000 network, whose main objectives are the protection of habitats and species considered vulnerable at the European level and their conservation in a favorable status (*sensu* 92/43/EEC "Habitats" Directive). However, this does not mean a total ban on human activities within these areas, but rather their integration. So, the creation of the N2000 network does not completely prevent access to these areas where, actually, various human activities can be carried out. Indeed, anthropic activities result to be the main driver of biological invasions (Early et al. 2016). Despite their protection Guerra et al. (2018) found out that N2000 sites are, actually, vulnerable to IAS. Recently, Lazzaro et al. (2020) showed that the scientific literature regarding the impacts and the invasion of IAPs in Italy is still incomplete and there are no data for many N2000 taxa and habitats, and that there is a gap of knowledge on the threats to which many habitats might be exposed due to alien plant invasion.

Accordingly, within this article we aimed to map the distribution of these six priority IAPs and identify which vegetation types and N2000 habitats (*sensu* 92/43/EEC "Habitats" Directive) are most invaded. For each species, through a series of field surveys, we monitored and updated previous data with the aim of producing an updated distribution map. Then we assessed the extent of the invaded areas and evaluated whether these included N2000 habitats. Additionally, we analyzed environmental data, such as slope, slope aspect, distance from human infrastructure and altitude, to investigate if there was a relationship between these factors and alien species distribution.

The information collected by means of this research is pivotal to define an ecological framework for future management actions to be carried out on Capraia Island.

Methods

Study area

Capraia Island (WGS84: 43°2'58.29"N, 9°50'6.38"E) is the third largest island (19.2 km^2 of surface) of the Tuscan Archipelago (Fig. 1), located 26 km from the Corsican coast and 53 km from the Tyrrhenian coast. The island is predominantly mountainous (maximum altitude, Monte Castello at 445 m a.s.l.), with a Mediterranean climate

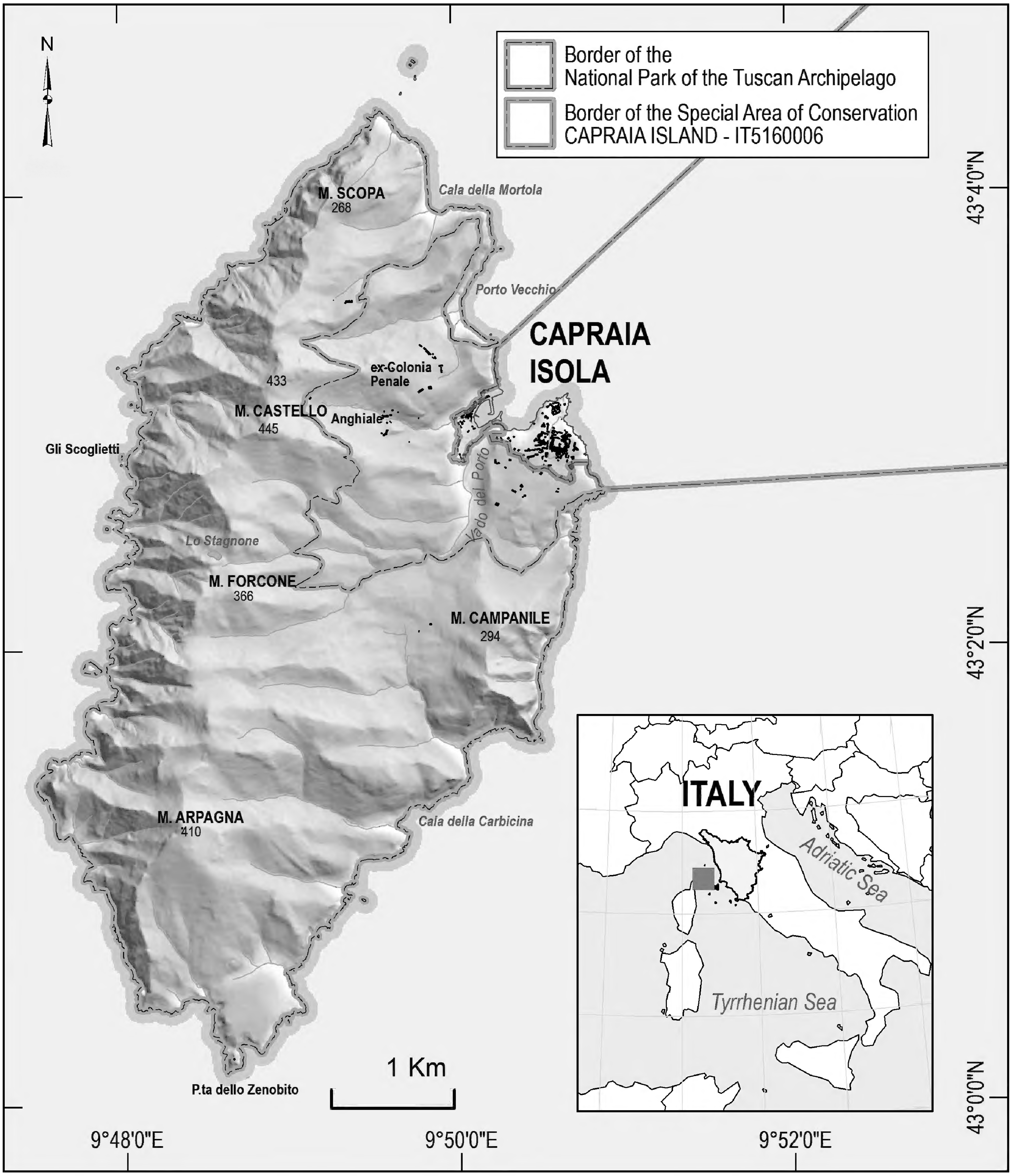

Figure 1. Study area, Capraia island. The grey line represents the border of the National Park of the Tuscan Archipelago, and the red line represents the border of the Special Area of Conservation CAPRAIA ISLAND – IT5160006 (WGS84, 4326 EPSG).

characterized by mild and rainy winters and hot and dry summers with a temperature peak in the months of July and August (Foggi and Grigioni 1999).

The vegetation is dominated by Mediterranean shrubland, while forest is almost absent (Foggi and Grigioni 1999). This is probably due to a constant and long-lasting anthropogenic pressure which probably began already with the Etruscans (Foggi and Grigioni 1999). Capraia Island also hosted a penal colony until the 1980s when intense agricultural activities were still carried out by the prisoners (PNAT 2021). Excluding the small nuclei of holm oak woodland, the most mature plant community is represented by the *Erico arboreae–Arbutetum unedonis* evergreen maquis, while the steep and rocky areas show less evolved vegetation stages from the same Mediterranean series (Lower meso-Mediterranean series of *Quercus ilex* on siliceous substrate, see Foggi and Grigioni 1999). After the ceasing of traditional land management, due to the succession processes taking

place in the abandoned areas, local vegetation is still characterized by a strong dynamism and high floristic diversity and patchiness. The island hosts a typical Mediterranean flora with a striking prevalence of therophytes followed by hemicryptophytes and phanerophytes (Foggi et al. 2001). The local endemism rate is considerable, including some restricted endemics and several broader endemics also occurring elsewhere in the Tuscan Archipelago, in Sardinia-Corsica and in the Tyrrhenian area.

Capraia Island is almost totally included in the Special Areas of Conservation (SAC)/Special Protection Areas (SPA) (IT5160006), which extends for 19 km^2, except for the port area and the inhabited center. Furthermore, 77% of the island territory belongs to the Tuscan Archipelago National Park. The island hosts 14 terrestrial habitats of conservation interest (*sensu* 92/43/EEC "Habitats" Directive) of which two are priority, i.e. 6220* "Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*" and 3170* "Mediterranean temporary ponds" (see Table 1 and Suppl. material 1 for a complete list of vegetation types and habitats taken into account for the analyses).

Species distribution mapping

The entire island was investigated with extensive field explorations focused on areas where the presence of six plant alien species (*Chasmanthe floribunda*, *Nicotiana glauca*, *Opuntia ficus-indica*, *Opuntia stricta*, *Senecio angulatus*, and *Zantedeschia aethiopica*; see Fig. 2, Table 2 for more details) was recorded in previous investigation (Lazzaro et al. 2014). Accordingly, to build an updated map of the current distribution of the six IAPs, we collected, reported and georeferenced punctual and spatial data, using the OruxMaps v.7.4.23 smartphone application and a map of Capraia Island at the 1:3000 scale. The field surveys were carried out during spring and summer 2021.

Due to the remarkable spread of both species of *Opuntia*, *O. ficus-indica* and *O. stricta*, we classified the areas invaded by them into density classes according to a logarithmic scale with 5 intervals: class 1 = 1–10 individuals per hectare, class 2 = 10–100 individuals per hectare (50 average individuals estimated), class 3 = 100–1000 individuals per hectare (550 average individuals estimated),

Table 1. Vegetation types and N2000 habitat (*sensu* 92/43/EEC "Habitats" Directive) present in Capraia Island. The first column represents the macro-categories of vegetation used for our analysis while the second column represents the N2000 habitats corresponding to or included within the macro-vegetation categories. All these data come from the cartographic analysis carried out for the SAC Management Plan (PNAT 2021).

Macro-Vegetation types	N2000 Habitats as described in PNAT (2021)	NOTE
Tall scrub with *Erica* sp. and *Arbutus unedo*	-	-
Orchards and tree crops	-	-
Riparian *Nerium oleander* galleries	92D0	Fully corresponding to the habitat
Low scrubs with *Cistus* sp. and/or *Erica* sp. and their mosaics	3120; 3170*; 6220*; 8220; 8230	Habitats with partial cover in the mosaic of vegetation
Mosaics of Mediterranean xeric grasslands and Mediterranean temporary ponds	6220*; 8220; 8230	Habitats with partial cover in the mosaic of vegetation
Mosaics of siliceous cliffs vegetation and Mediterranean xeric grasslands	6220; 3120; 3170*	Habitats with partial cover in the mosaic of vegetation
Euphorbia dendroides scrub	5330	Fully corresponding to the habitat
Scrub mosaics with *Euphorbia dendroides*, *Erica* sp. and *Cistus* sp.	5330	Habitat with partial cover in the mosaic of vegetation
Vegetation of abandoned areas	6220*	Habitat with partial cover in the mosaic of vegetation
Artificial pine forests	-	-
Coastal vegetation	1240; 1430; 3120; 3170*; 5330; 5320; 8220	Habitats with partial cover in the mosaic of vegetation
Quercus ilex forests and thickets	9340	Fully corresponding to the habitat
Acquatic vegetation of the Stagnone pond	3120; 3140; 3150; 6420	Fully corresponding to a mosaic of this habitats

Table 2. Summary table showing the different biological and ecological characteristics of the six target invasive species on Capraia Island (Weber 2017).

Species	Families	Area of origin	Life-form	Dispersal means	Reproduction system	Introduction pathway
Opuntia stricta (Haw.) Haw.	*Cactaceae*	Southern USA, Caribbean	Succulent perennial	Animals	Vegetative and sexual	Fruit-producing
Opuntia ficus-indica (L.) Mill.	*Cactaceae*	Central America, Mexico	Succulent perennial	Animals	Vegetative and sexual	Fruit-producing
Senecio angulatus L. f.	*Asteraceae*	South Africa	Perennial herb	Wind	Vegetative and sexual	Ornamental purpose
Nicotiana glauca Graham	*Solanaceae*	Southern America	Evergreen shrub, tree	Animals	Vegetative and sexual	Ornamental purpose
Chasmanthe floribunda (Salisb.) N.E.Br	*Iridaceae*	South Africa	Perennial herb	Animals	Vegetative and sexual	Ornamental purpose
Zantedeschia aethiopica (L.) Spreng	*Araceae*	South Africa	Prennial herb	Water, animals	Vegetative and sexual	Ornamental purpose

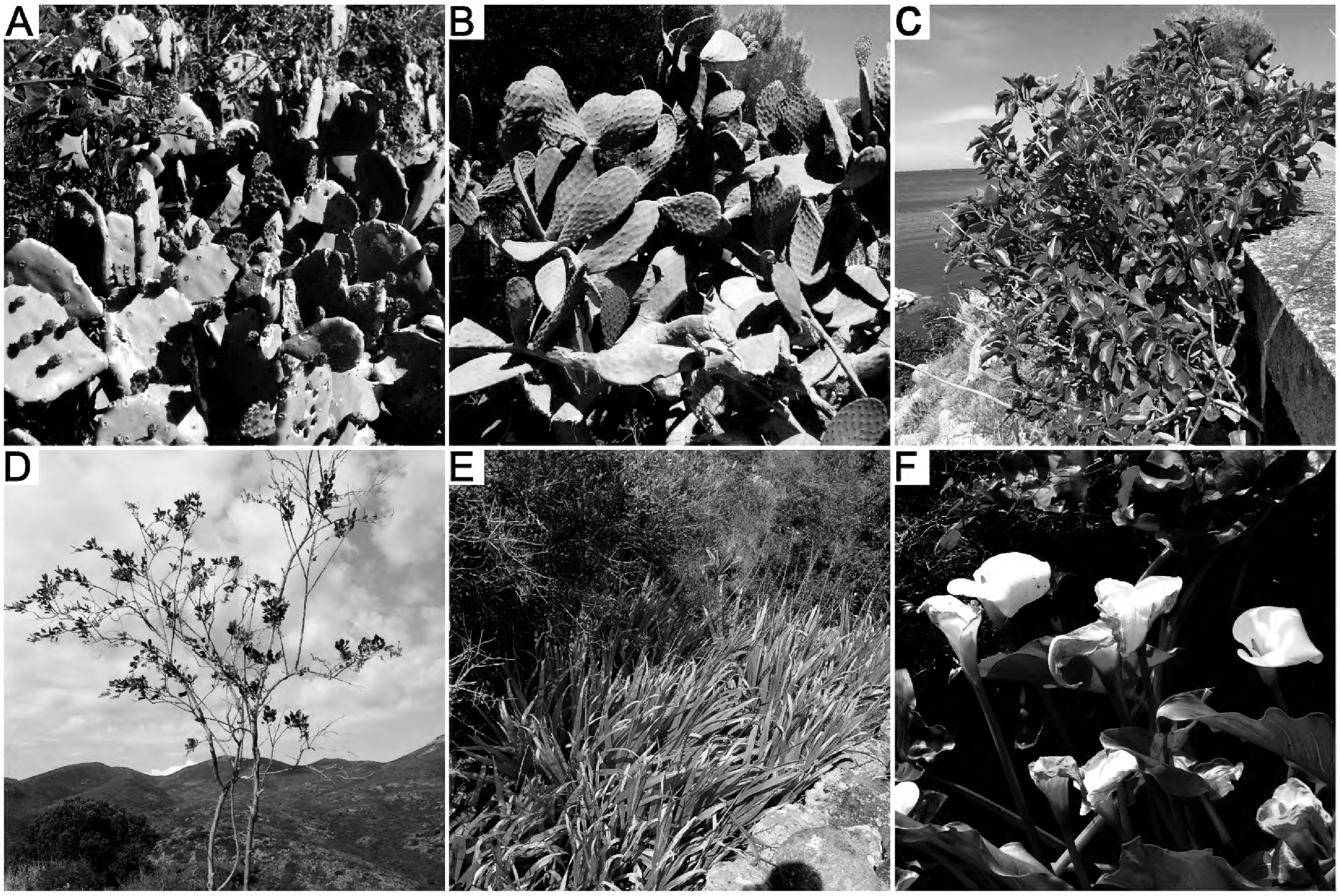

Figure 2. Some images of the six invasive alien species at Capraia Island: **A.** *Opuntia stricta*; **B.** *Opuntia ficus-indica*; **C.** *Senecio angulatus*; **D.** *Nicotiana glauca*; **E.** *Chasmanthe floribunda* and **F.** *Zantedeschia aethiopica.*

class 4 = 1000–4000 individuals per hectare (2500 average individuals estimated), and class 5 >4000 individuals per hectare (10000 average individuals estimated). These estimates of individuals do not correspond to an actual mathematical average, but rather to empirical estimates performed approximately through visual observation carried out in the field, aided by binoculars for the inaccessible areas of the island. As for the other study species, we considered square meters of invaded area, since these are species that create monospecific mats.

Data collection and analysis

After collecting the data in the field, the IAPs distributional data were reported into geographic information systems (GIS) environment using ArcGIS Software vers. 10.8.1 (https://desktop.arcgis.com). The digitization was aided with the use of the land aerial photos of the Tuscany Region, OFC 2019 20 cm - 32 bit color – RGB and OFC 2016 20 cm - 32 bit color – RGB (available at https://www502.regione.toscana.it/geoscopio/ortofoto.html) and other satellite orthophoto sources, Google Satellite and Bing Virtual Earth. Distribution data were initially digitized using two vectorial topologies, points and polygons, the first for punctual data and the other for polygonal data. The point data were used in the case of small areas or few individuals that could not be reasonably outlined on the field maps during the surveys due to scale constraints, noting the areas extension and position. To allow further analyses of the spatial extent of the plant distribution, punctual data were then transformed into polygonal data and then merged with them, to obtain a single polygonal geographic feature of the distribution of IAPs. From this geographical layer we extrapolated the current extent of the surface invaded by each species.

To assess which vegetation types and N2000 habitats were mostly invaded, we retrieved the latest updated cartographic data concerning the vegetation and N2000 habitats on the island, issuing from the cartographic analysis included in the SAC Management Plan (PNAT 2021). To achieve a better graphical rendering and analysis at finer scale, we merged the vegetation types into 13 macro-categories (see Table 1 and Suppl. material 1). The layers obtained for vegetation and N2000 habitats were superimposed and merged with the layer of the distribution of IAPs through a spatial join. Finally, we calculated from the obtained geographical layers the current extent of the invaded surface for each vegetation type and N2000 habitat.

Ultimately, we explored the connection between and the IAPs distribution and environmental factors. We studied the species presence/absence in a 10 × 10 m cell grid in function of the following environmental factors: slope, slope aspect, distance from human infrastructure and altitude, using a Generalized Linear Model (GLM) with binomial distribution of the errors. Slope aspect was

expressed as northerness following the formula: northerness = cosine [(aspect in degrees * π)/180)]. The analyses were conducted in R environment (R version 4.2.3) and the graphs were produced using the ggplot2 R package version 3.4.2 (Wickham 2016).

Results

The total invaded area amounts to about 71 ha (3.6% of the island's area). The most widespread species resulted to be *Opuntia stricta* with over 70 ha, while *Nicotiana glauca* is the least common one with 51 m^2 in the island (Table 3). The six alien species are mainly located in the north-eastern area of the island, the one more prone to anthropogenic disturbance, and they also spread within the SAC. *Opuntia stricta* is the only species that spreads significantly outside the town in areas with natural vegetation, reaching the territories of the National Park in small and scattered patches (Fig. 3). The most threatened vegetation types are: "Low scrubs with *Cistus* sp. and/or *Erica* sp. and their mosaics", "Coastal vegetation", "Urbanized areas", "*Euphorbia dendroides* scrub" and "Scrub mosaics with *Euphorbia dendroides*, *Erica* sp. and *Cistus* sp." (Figs 4, 5). It worths being highlighted that "*Euphorbia dendroides* scrub" and "Scrub mosaics with *Euphorbia dendroides*, *Erica* sp. and *Cistus* sp." are invaded only by *Opuntia stricta*, which is by far the most common species in the "Coastal vegetation". Moreover, the "Low scrubs with *Cistus* sp. and/or *Erica* sp. and their mosaics" and the "Urbanized areas" host all the invasive alien species considered in this study (Fig. 5). Focusing only on *O. stricta* distribution, our results show that all the vegetation types present the density class 2, which is one of the most representative in terms of total surface area together with classes 3 and 4. Instead, class 5 is found in the "Urbanized areas" and in the "Coastal vegetation" (Fig. 6).

As far as N2000 habitats are concerned, *Chasmanthe floribunda*, *Nicotiana glauca*, *Opuntia stricta*, *Senecio angulatus* and *Zantedeschia aethiopica* show a different distribution pattern. The most invaded habitat is 5330 "Thermo-Mediterranean and pre-desert scrub", with 10 ha massively occupied by *Opuntia stricta*. The other invaded habitats are: 5320 "Low formations of *Euphorbia* close to cliffs", 1240 "Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp." and 6220* "Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*".

Concerning the other species, *Senecio angulatus* is mostly found in 1240 habitat, and it occurs forming very small patches in 3120 habitat "Oligotrophic waters containing very few minerals generally on sandy soils of the West Mediterranean, with *Isoëtes* spp." and in the 3170* priority habitat "Mediterranean temporary ponds". Instead, *Zantedeschia aethiopica* is present within the 92D0 habitat "Southern riparian galleries and thickets (*Nerio-Tamaricetea* and *Securinegion tinctoriae*)". Finally, *Chasmanthe floribunda* and *Nicotiana glauca* invade a truly irrelevant portion of habitat 6220*, 3170* and 3120 respectively (Table 4). Focusing on the *Opuntia* spp. distribution in N2000 habitats, we note that most invaded ones are the same above (5330, 5320, 1240 and 6220*), while the most represented classes are 2, 3 and 4 (Fig. 7).

For all the alien species we found a significant and negative correlation among the probability of presence and the distance from human infrastructure, with a higher presence closer to human settlements. Altitude has a significant effect on the alien species *Opuntia stricta*, *Chasmathe*

Table 3. Area invaded at Capraia Island by the six alien species examined. The whole invaded area amounts to about 71 ha (3.6% of the island's area). The most widely distributed species is *Opuntia stricta* with over 70 ha, while *Nicotiana glauca* is the least widespread with 51 m^2 in the island.

Species	Invaded area (m^2)
Chasmanthe floribunda	445,41
Nicotiana glauca	50,56
Opuntia ficus-indica	971,05
Opuntia stricta	708875,10
O. stricta density class 1	114107,63
O. stricta density class 2	294136,26
O. stricta density class 3	145594,30
O. stricta density class 4	147219,49
O. stricta density class 5	7817,42
Senecio angulatus	1291,04
Zantedeschia aethiopica	234,08
Tot	711867,24

Table 4. Areas invaded by *Opuntia stricta*, *Senecio angulatus*, *Chasmanthe floribunda*, *Nicotiana glauca* and *Zantedeschia aethiopica* at Capraia Island divided into N2000 habitats.

Habitat	*Chasmanthe floribunda*	*Nicotiana glauca*	*Opuntia stricta*	*Senecio angulatus*	*Zantedeschia aethiopica*	Total m^2
1240			17839.77	18.12		17857.90
3170*		0.01	1207.80	1.60		1209.41
5320			23798.82			23798.82
5330			100449.38			100449.38
6220*	0.51		12782.86			12783.37
8220			1349.52			1349.52
92D0			271.39		48.86	320.25
3120		0.01	875.45	1.60		877.06
8230			0.03			0.03
Total m^2	**0.51**	**0.01**	**158575.03**	**21.32**	**48.86**	**158645.73**

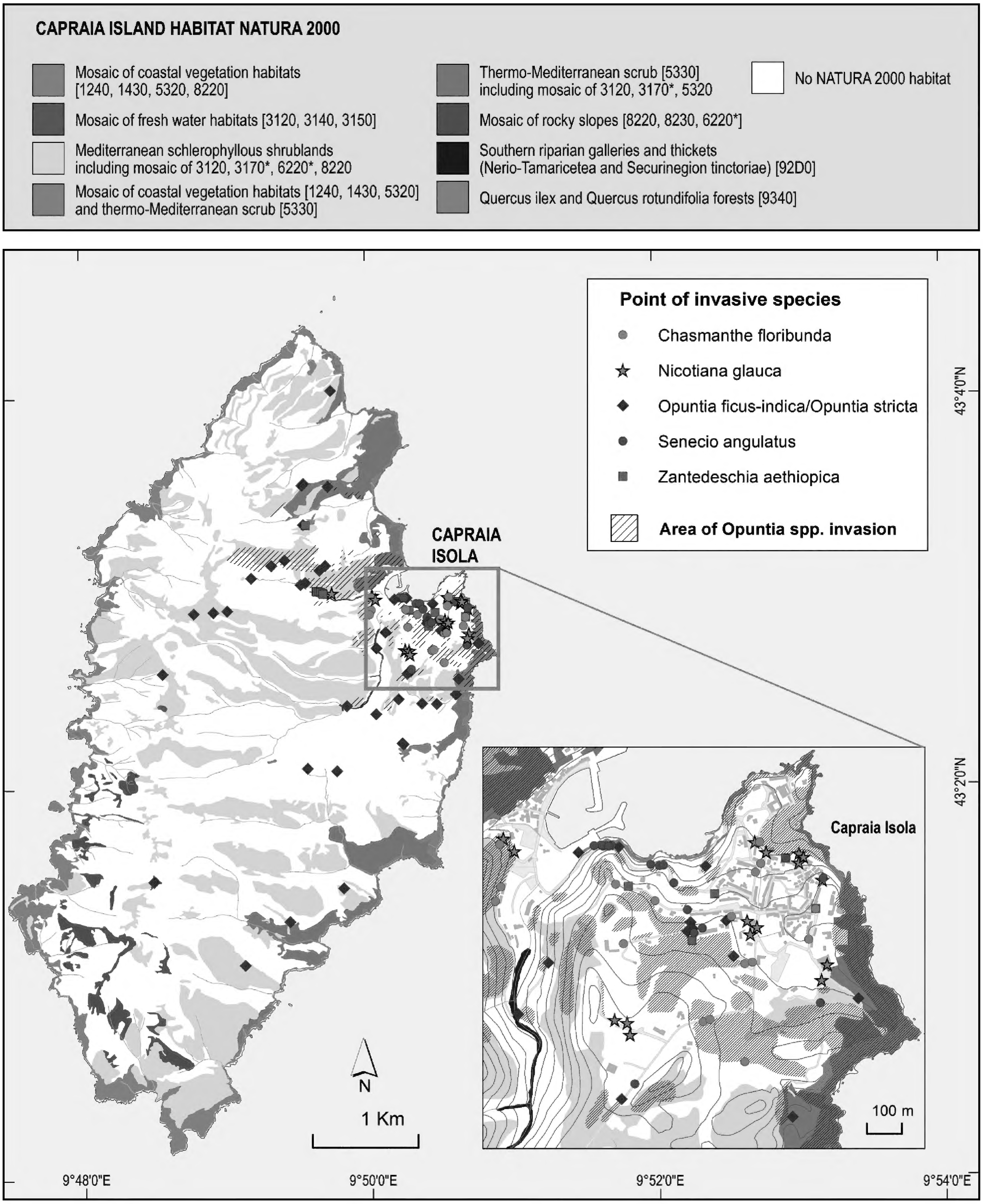

Figure 3. Current distribution map (WGS84, 4326 EPSG) of the six alien species *Opuntia stricta*, *O. ficus-indica*, *Senecio angulatus*, *Chasmanthe floribunda*, *Nicotiana glauca* and *Zantedeschia aethiopica* at Capraia Island with respect to N2000 habitats (sensu Habitats Directive, 92/43/EEC). WGS84.

floribunda, *O. ficus-indica*, and *Senecio angulatus* showing a higher probability of occurrence at lower altitudes, near the sea. Only for *Opuntia stricta*, *O. ficus-indica* and *Senecio angulatus* we found a significant effect of slope aspect, with *O. stricta* growing preferably in south-facing areas, while *O. ficus indica* and *Senecio angulatus* in north-facing areas. Finally, *Nicotiana glauca*, *Opuntia ficus-indica*, and *Senecio angualtus* seem to prefer areas further from steep cliffs, showing a significant and negative correlation with slope (Fig. 8 and Table 5).

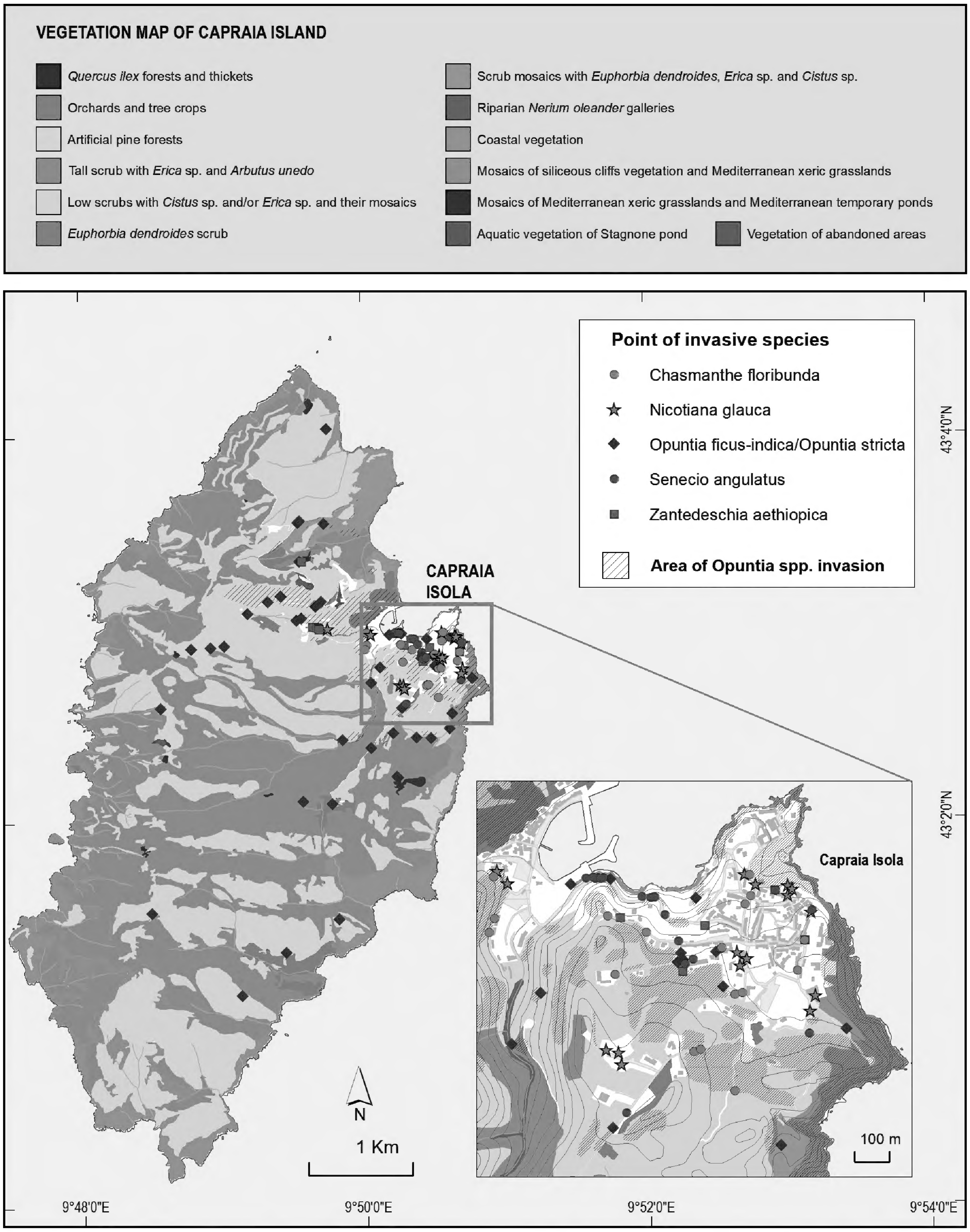

Figure 4. Current distribution map (WGS84, 4326 EPSG) of the six alien species *Opuntia stricta*, *O. ficus-indica*, *Senecio angulatus*, *Chasmanthe floribunda*, *Nicotiana glauca* and *Zantedeschia aethiopica* at Capraia Island with respect to vegetation type. WGS84.

Discussion

The results of our study provide a detailed picture of the current status of plant invasions at Capraia Island through an accurate field check on the distribution of the main IAPs. Almost 4% of the island's surface is invaded by the six alien species analyzed, of which the most widespread is *Opuntia stricta* with over 70 ha, while the most threatened habitats are 5330, 5320, 1240 and 6220*. Notably, the habitat 5330, characterized by the dominance of *Euphorbia dendroides*, is a relatively rare Mediterranean habitat in Italy, reaching its highest latitudinal extent along the northern border of the peninsula, particularly in Liguria and Tuscany. The four aforementioned habitats are often in close spatial contact with each other and are all typical of Mediterranean areas with hot and dry summers. This likely contributes to their suitability for the establishment and spread of *Opuntia stricta*, a species well-adapted to these environmental conditions as it is thermophilic, xerophilic and heliophilous with CAM metabolism and specialized organs for water reserve (Nobel 2002; Novoa et al. 2015). Furthermore, *O. stricta* can very easily propagate vegeta-

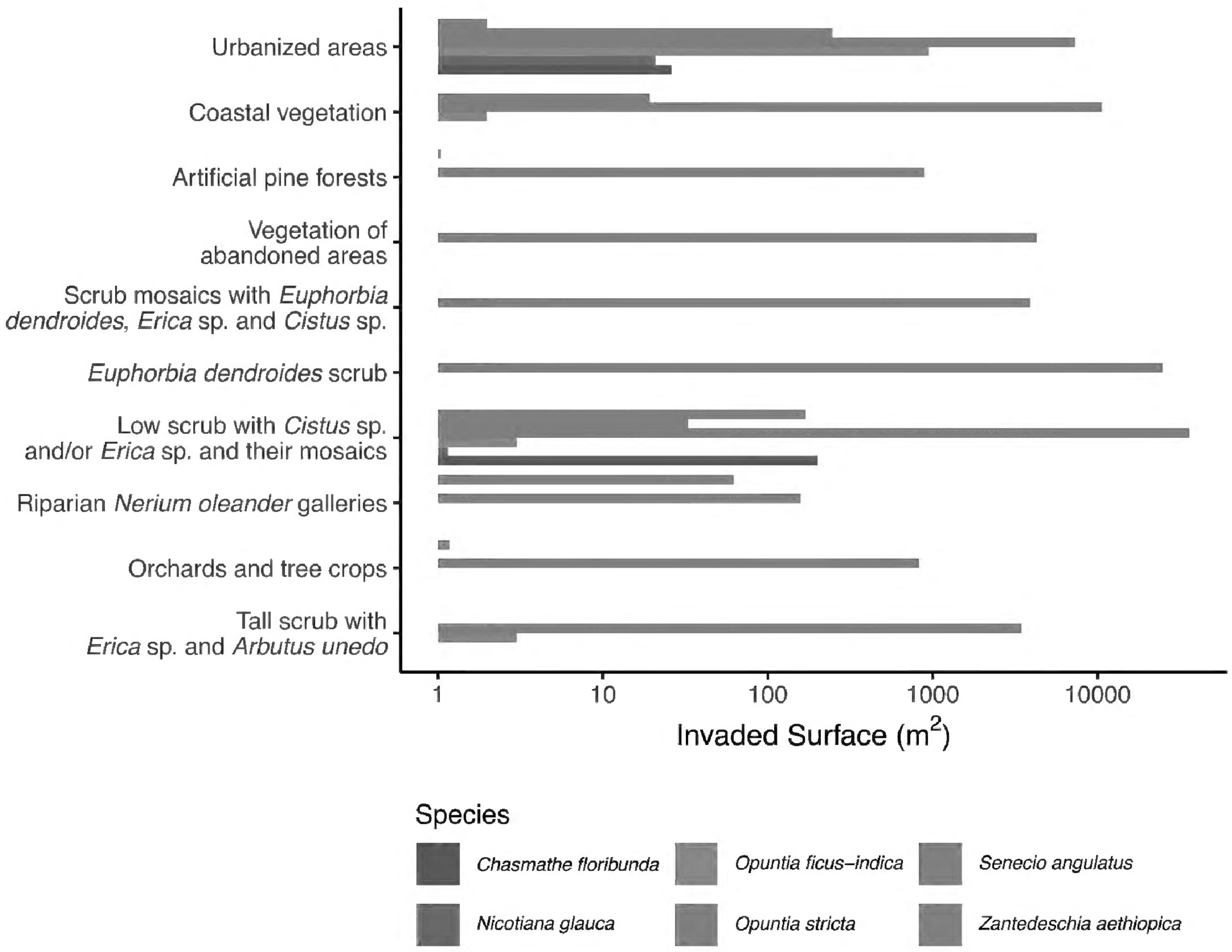

Figure 5. Total area invaded by the six species *Opuntia stricta*, *O. ficus-indica*, *Senecio angulatus*, *Chasmanthe floribunda*, *Nicotiana glauca* and *Zantedeschia aethiopica* at Capraia Island per vegetation type.

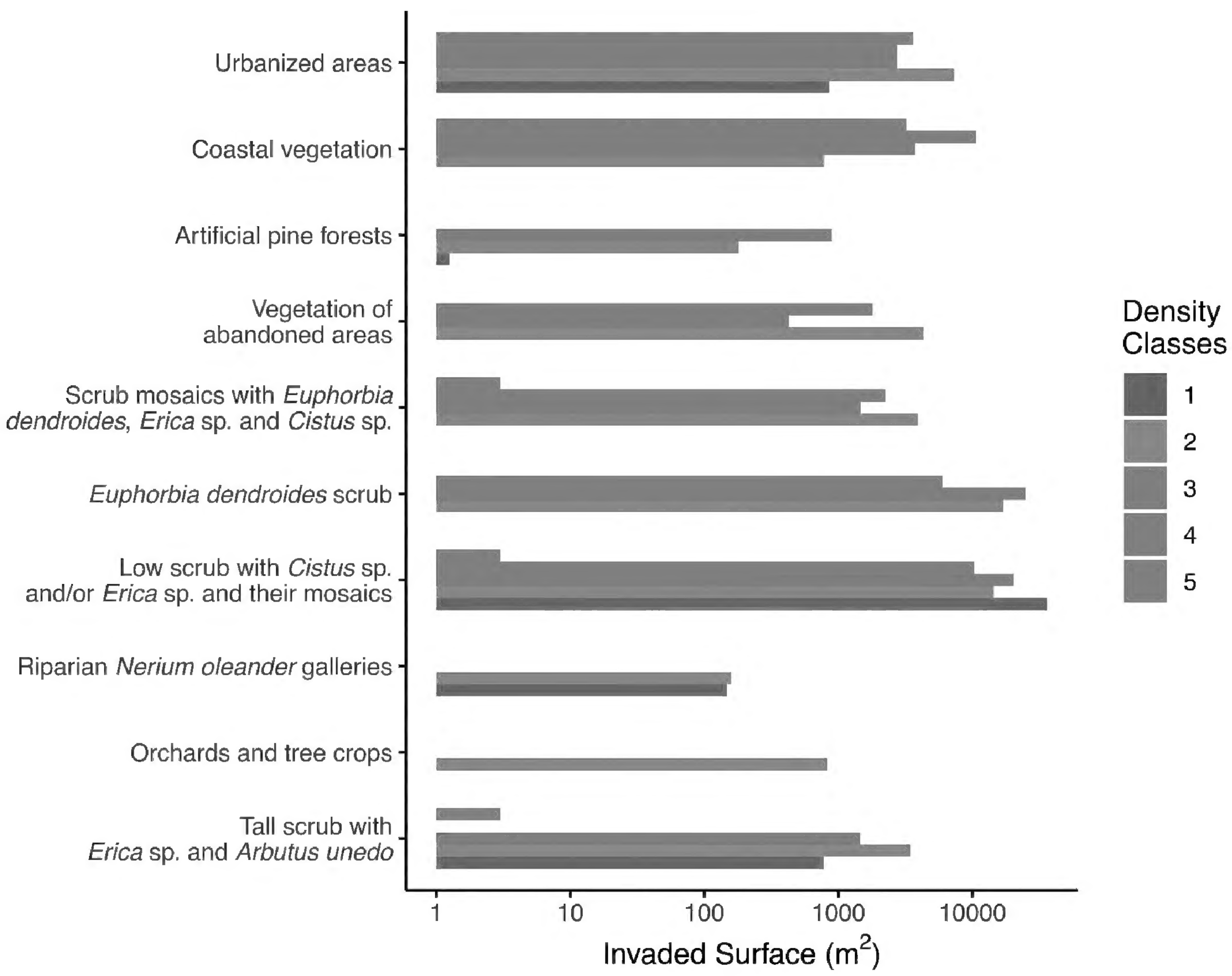

Figure 6. Area invaded by *Opuntia stricta* and *O. ficus-indica* divided into density classes by vegetation type. Density classes according to a logarithmic scale with 5 intervals: class 1 with 1–10 individuals per hectare, class 2 with 10–100 individuals per hectare (50 average individuals estimated), class 3 with 100–1000 individuals per hectare (550 average individuals estimated), class 4 with 1000–4000 individuals per hectare (2500 average individuals estimated), and class 5 with >4000 individuals per hectare (10000 average individuals estimated).

tively through fragmentation of cladodes and by seeds, spreading even over medium to long distances by birds and mammals, footwear and vehicles (Sheehan and Potter 2017; Weber 2017). During our field surveys, we observed directly that *Corvus corax* feeds on *O. stricta* fruits (pers. obs. Michele Giunti), and it is conceivable that also mouflon *Ovis orientalis* and the black rat *Rattus rattus*, both alien species in Capraia Island, can act as dispersers, too. New investigations should be encouraged to delve deeper into the dispersion mechanisms of this species.

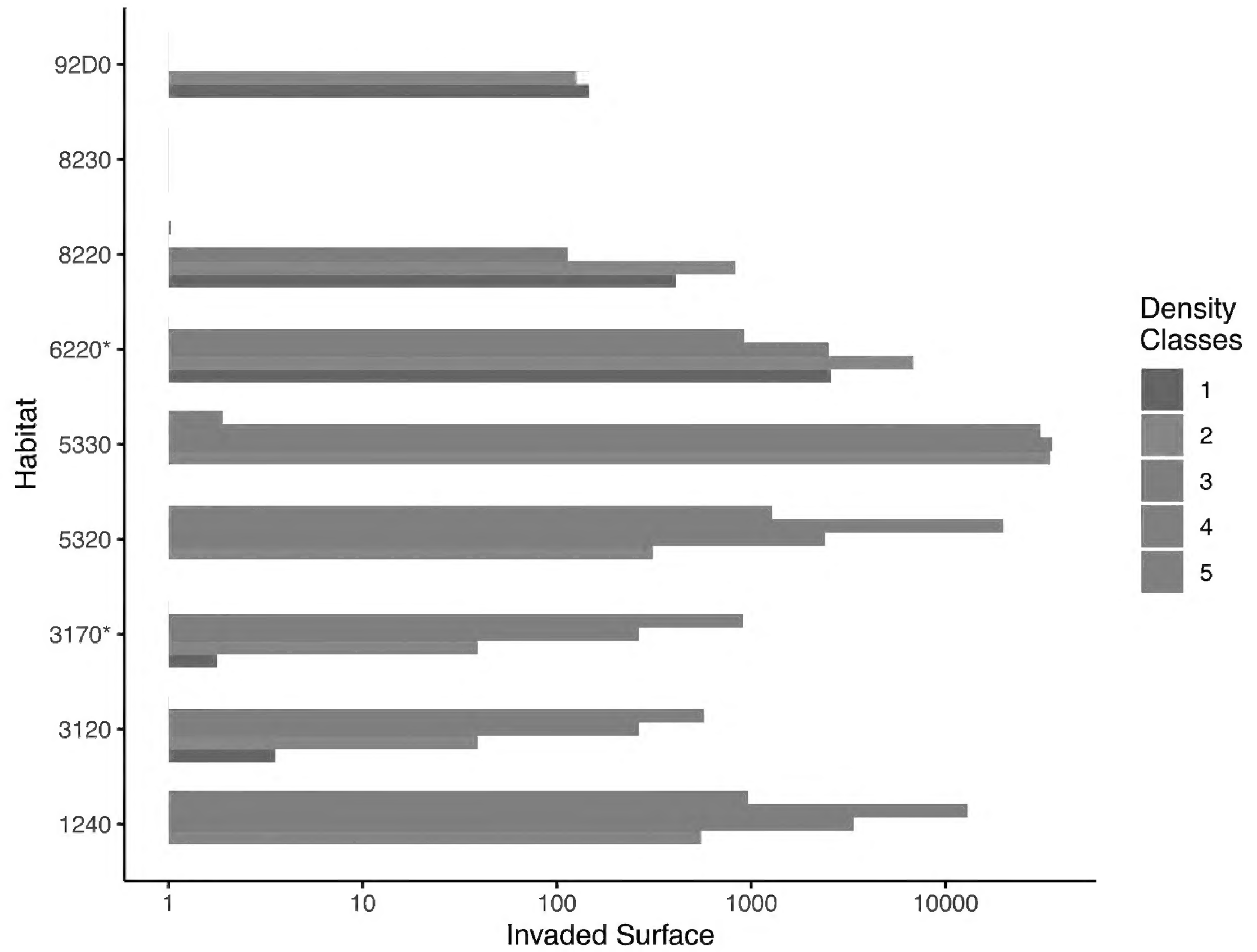

Figure 7. Areas invaded by *Opuntia stricta* and *O. ficus-indica* divided into N2000 habitats (sensu Habitats Directive, 92/43/EEC) and density classes. Density classes according to a logarithmic scale with 5 intervals: class 1 with 1–10 individuals per hectare, class 2 with 10–100 individuals per hectare (50 average individuals estimated), class 3 with 100–1000 individuals per hectare (550 average individuals estimated), class 4 with 1000–4000 individuals per hectare (2500 average individuals estimated), and class 5 with >4000 individuals per hectare (10000 average individuals estimated).

Table 5. Repeated Measurement ANOVA table to analyse the relationship between environmental factors (distance from infrastructure, northerness, altitude and slope) and the six invasive species. Significance codes: p value < 0.001 '***'; p value < 0.01 '**'; p value < 0.05 '*', p value < 0.10 '.'.

Species	Enviromental factors	Df	Deviance Resid.	Df Resid.	Dev	Pr(>Chi)	
Opuntia stricta	Distance from infrastructure	1	25092.40	193714	45537.00	<0.001	***
	Northerness	1	3547.80	193713	41989.00	<0.001	***
	Altitude	1	1841.00	193712	40148.00	0.014	*
	Slope	1	1125.80	193711	39022.00	0.054	
Chasmanthe floribunda	Distance from infrastructure	1	213.40	193714	545.38	<0.001	***
	Altitude	1	24.80	193713	520.54	<0.001	***
Nicotiana glauca	Distance from infrastructure	1	161.99	193714	263.45	<0.001	***
	Slope	1	4.10	193713	259.40	<0.001	***
Senecio angulatus	Distance from infrastructure	1	330.15	193714	645.44	<0.001	***
	Northerness	1	70.82	193713	574.62	<0.001	***
	Altitude	1	40.15	193712	534.47	<0.001	***
	Slope	1	25.90	193711	508.57	<0.001	***
Zantedeschia aethiopica	Distance from infrastructure	1	100.65	193714	288.07	<0.001	***

Although there are numerous specific case studies investigating the distribution of some IAPs (e.g. Bogdanovi et al. (2006) *for Nicotiana glauca* in Croatia), in Europe their effects on native plant communities of N2000 habitats have been poorly explored and underestimated (Guerra et al. 2018). Regarding Italy, Lazzaro et al. (2020) pointed out that these knowledge gaps also occur at the national level, showing a lack of data homogeneity between Italian regions, a lack of evidence even for well-known invasive species and, finally, a lack of data on the impacts of IAPs on N2000 habitats.

As to coastal and island ecosystems, while several articles evaluated the impacts of IAPs on coastal sand dune environments (e. g. Del Vecchio et al. 2013; Sperandii et al. 2018; Sarmati et al. 2019; Cascone et al. 2021; Giulio et al. 2021), the impacts on sea cliff communities are still understudied compared to the other types of coastal habitats (Mugnai et al. 2022). In Giglio Island, also part of the Tuscan Archipelago, rocky cliff habitats, especially 1240 and 5320, were investigated and considered to be among the most threatened by invasive plants, particularly *Carpobrotus* species (Mugnai et al. 2022). As for

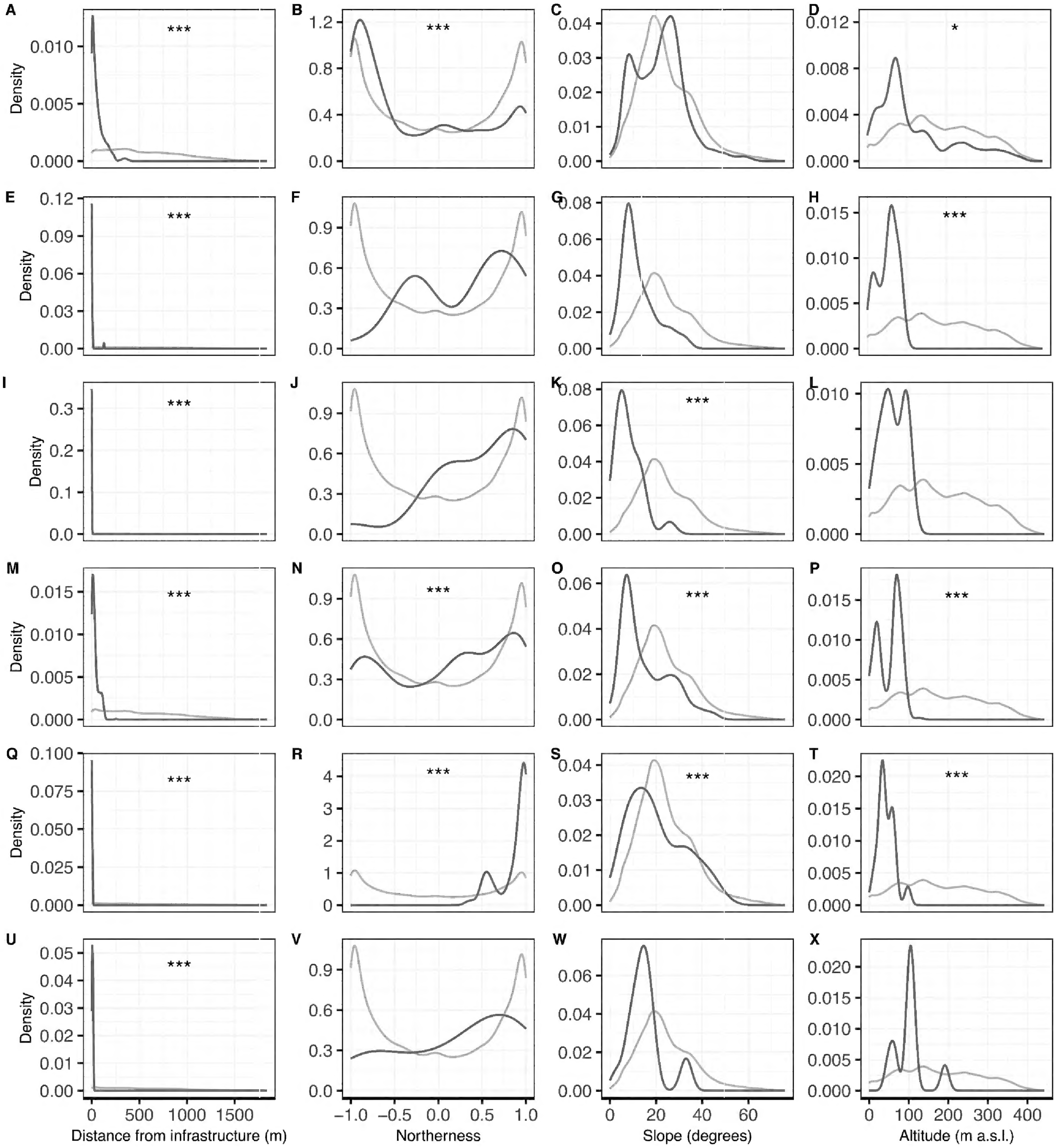

Figure 8. Variation of the alien species density and the environmental factors (distance from infrastructure, northerness, slope and altitude): *Opuntia stricta* (**A, B, C, D**), *Chasmanthe floribunda* (**E, F, G, H**), *Nicotiana glauca* (**I, J, K, L**), *Opuntia ficus-indica* (**M, N, O, P**), *Senecio angulatus* (**Q, R, S, T**), *Zantedeschia aethipica* (**U, V, W, X**).

Capraia Island, urban, suburban and semi-natural areas and habitats with greater anthropic disturbance are the most invaded. Indeed, for example, they represent the focal points of spread also on Linosa Island (Pelagie Islands, Sicily) (Pasta et al. 2017). Unlike what was found on Capraia, in Linosa the plant communities belonging to 6220*, 5330 and 5320 habitats were less susceptible to alien plant invasion than those of other habitats. In fact, on Linosa, the most invasion-prone habitats were the habitat 8220 "Siliceous rocky slopes with chasmophytic vegetation" and the habitat 8320 "Fields of lava and natural excavations" (Pasta et al. 2017). In some islands and mainland locations in Spain, highly disturbed areas near old houses and in abandoned fields are where *Opuntia* species are most commonly found (Padrón et al. 2011; Gómez-Bellver et al. 2020). Furthermore, the presence of *Opuntia maxima*, *O. dillenii* and *O. stricta* was reported in rocky coastal habitats and in Mediterranean scrub mixed with abandoned fields (Padrón et al. 2011).

Novoa et al. (2015) reported that the invasion of cacti is most commonly documented for Australia, South Africa and Spain and that one of the most widespread invasive

species is *O. ficus-indica*. Furthermore, they reported that cacti are among the most harmful invasive alien plants and that there is an over-increasing interest in many cacti for ornamental purposes, predicting many new invasion events in the future. Event confirmed by Gómez-Bellver et al. (2020) who mentioned the spread of a new neophyte, *Opuntia aurantiaca*, present only in Europe on the Mediterranean coast of the Iberian Peninsula (Catalonia and Valencian Community).

Out of the six IAPs examined, five (*Nicotiana glauca*, *Opuntia ficus-indica*, *O. stricta*, *Senecio angulatus* and *Zantedeschia aethiopica*) emerged as invasive species posing significant threats, as indicated by two risk assessments conducted on alien plant species within the Tuscan Archipelago (Lazzaro et al. 2016). While the remaining, *Chasmathe floribunda*, was identified as a species of minor concern. The abundance of the six IAPs analyzed is also different across the Tuscan Archipelago (Lazzaro et al. 2014). For example, *Opuntia ficus-indica* and *Senecio angulatus* are notably widespread in the entire Archipelago. However, despite its largest recorded presence on Capraia, *Opuntia stricta* exhibits limited distribution with only a report in Giglio Island.

All six target species show an ecological preference for low-altitude areas close to the coastline and areas characterized by high levels of human disturbance. The significant influence of human activity, expressed both as tourist pressure and the expansion of settlements, on the richness and composition of alien flora in small Mediterranean islands is clearly emphasized in literature (McMaster 2005; Kueffer et al. 2010; Pretto et al. 2012). Nevertheless, the association with other environmental factors is not consistently evident and may depend on the ecological or biological traits of the species. For example, as for *O. stricta*, while Foxcroft et al. (2007) reported that there are no clear variables to explain its distribution pattern and that no specific environmental factors are decisive or predicting *O. stricta* density in Kruger National Park, we found a stronger suitability of southern slopes,. The high temperatures typical of Capraia (see Foggi and Grigioni 1999) could promote the germination of *Nicotiana glauca* and *Opuntia ficus-indica* and partially explain their establishment and spread on the island. In fact, for *Nicotiana glauca*, Florentine et al. (2016) reported that the highest germination values were observed in seeds exposed to alternating temperatures (30–20 °C) and 12/12 h light/dark regimes. Likewise, similar temperature ranges (20–25 °C) showed to be the optimum also for the germination of *Opuntia ficus-indica* (Podda et al. 2017). In addition, the ability of its seeds to germinate at high NaCl concentrations may be pivotal to sustain its spread close to the coastline areas and in soils with high salt concentrations.

Conclusion

In conclusion, this study contributes to a better knowledge of the N2000 habitats invaded by the main six alien species in Capraia Island. We reported the most threatened habitats and gave a complete picture of the current invasion process in Capraia, which shows no signs of slowing down. Precisely for this reason, although *O. stricta* is currently the only species on which there is no doubt about the urgency of timely management intervention, it is also important to consider that currently its impact mechanisms and outcomes on native plant communities are not well known.

Because of the importance of a more in-depth study to apply effective management strategies, we are conducting new research to better understand the impact mechanisms exerted on some N2000 habitats by *Opuntia stricta*, the most widespread species on Capraia Island. Finally, it would be important to monitor the invasive capacity of the other species and investigate the possible effects of their invasion, aware that the longer the time interval from the moment of introduction, the more difficult and costly possible future interventions are.

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Supplementary material 1

Vegetation types and N2000 habitat (sensu Habitats Directive, 92/43/EEC) present in Capraia Island

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Data type: docx

Explanation note: **table S1.** Vegetation types and N2000 habitat (sensu Habitats Directive, 92/43/EEC) present in Capraia Island. The first column represents the macro-categories of vegetation used for our analysis which include both the most specific vegetation types in the second column and N2000 habitats in the third column, both coming from the cartographic analysis carried out for the SAC Management Plan (PNAT 2021).

Link: https://doi.org/10.3897/pls2024611/02.suppl1